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ALLOMETRIC STUDIES ON ENERGY RELATIONSHIPS IN THE SPIDER CRAB *LIBINIA EMARGINATA* (LEACH)[1]

JOHN CARLSON ALDRICH [2]

*Boston University Marine Program, Marine Biological Laboratory,
Woods Hole, Massachusetts 02543*

Allometry, in the extended sense employed by Gould (1966), is the study of variables exhibiting differential growth. These variables may be morphological (*e.g.,* width/length), physiological (*e.g.,* size/oxygen consumption), or chemical (*e.g.,* size/lipid weight); and the relationships may be dynamic, as in successive measurements made on a growing animal, or they may be static, as in comparisons between non-growing adults.

Changes in the rates of differential growth have been found to accompany maturity in both vertebrates and invertebrates (Teissier, 1931, 1960; Needham, 1942; Brody, 1945; von Bertalanffy, 1957). In decapods, developing maturity is manifested at the molts of prepuberty and puberty (Hartnoll, 1963).

As an animal passes from an immature and actively growing stage to a mature, non-growing and reproducing stage, it is likely that its energy requirements change. Further, if an animal is found in different habitats correlated with successive stages of growth, it is likely that the energy available to it also changes. A succession of growth stages and their associated habitat changes have been termed growth stanzas (Parker and Larkin, 1959). It seemed likely that the energy requirements of a crab would be reflected in the differential growth of variables sensitive to energy requirements, with these differences especially marked when successive growth stanzas were compared.

Now, allometry facilitates the comparison of greatly varying sizes by reducing constant relative growth rates to a power function. The relationship of Y to X is allometric when $Y = bX^a$; where a is the rate of change of Y with respect to X, and b is the intercept, or size of Y when $X = 1$ (Huxley, 1924). Such relative growth rates appear on double-logarithmic plots as straight lines, with changes

[2] Present address: Department of Zoology and Comparative Physiolgy, Queen Mary College (University of London), Mile End Road, London E1 4NS, England.

in rates shown by inflections or discontinuities (Teissier, 1960), as is the case with morphological allometry during the transition from immature to mature stages in Maiid crabs (Hartnoll, 1963).

Hemmingsen (1950) suggested a theoretical limitation of metabolic rate based on the absorptive area of the digestive apparatus. For a crab such a relationship would be shown by similar constants for the slopes of oxygen consumption, stomach capacity, and hepatopancreas weight, this latter being the chief organ of digestion (Vonk, 1960). Such a comparison can be used for other purposes, especially if the sizes of the stomach (or its capacity), and the hepatopancreas (or its lipid content) can be shown to have a maximum likely value at a given size. Such maximum values would be represented by the upper bound of a scattergram of individual points. This is especially valid if the upper bound has the same slope as the overall average. Relative energy flow within a given growth stanza could then be shown by the average size of the organ measured, relative to the regression of the maximum size.

The organ in crabs that is apparently most sensitive to energy flow is the hepatopancreas, with lipids being the most labile constituent, probably reflecting overall energetic demands (Armitage, Buikema and Willems, 1972). This has been extensively studied in relation to the molt cycle by Drach (1939) and Renaud (1949), and has been looked at over growth stages in general in the crayfish *Orconectes nais* (Armitage *et al*, 1972).

This study was therefore designed to examine the allometric relationships of stomach capacity, the adequacy of natural feeding rates, and the size and lipid content of the hepatopancreas; both as related to the state of maturity of the crab reflected by its energetic demands, and the capacity of its habitats to supply these demands. The work done is presented in two major parts. In the first part (morphological allometry) the growth stages are defined by their allometric constants of external morphology, and by their associated habitats. In the second part (physiological allometry), oxygen consumption, stomach capacity and the proportion used, hepatopancreas total and lipid weights, average caloric intake, the cycling rate of stomach contents, and the efficiency of assimilation are treated, and the relative proportions of usage or energy flow computed for the stages previously described.

METHODS

Crabs

Specimens of *Libinia emarginata* (Leach), (Maiidae: Pisinae) the common spider crab of the east coast of the United States, were collected in the shallow waters within a radius of ten miles of Woods Hole, Massachusetts. Immature crabs, from 0.2 to 28 g were usually collected in masses of chlorophytous alga. The crabs clung to this coarse alga and covered themselves with finer filamentous chlorophytes and rhodophytes. Many of these crabs were found in a soft, newly-molted condition, indicating active growth in this habitat. Mature crabs were always collected on relatively barren mud or gravel bottoms, predominantly the former. These larger crabs ranged from 28 to 480 g. A naturalist's dredge was used to collect the immature crabs and an otter trawl for the mature ones. Specimens used for organ analyses were killed and examined within a few hours

of collection, others were kept in running seawater tanks and were used for feeding and respiration experiments. Throughout the testing and collecting period of July–September, 1971, the ambient seawater temperature remained between 20–22° C.

Allometry

General. When plotted on double-logarithmic axes, an allometric relation is shown by a straight line having the equation; $\log Y = a \log X + \log b$; where a is the slope of the allometric line and can be measured directly on the plot (Teissier, 1960). Such plots were used initially to identify relationships, but for purposes of statistical comparisons, least squares regressions were computed and F tests of slope (a) and level (b) made between lines. Strictly speaking, none of the regressions can be said to have an independent and a dependent variable, instead they covary with both variables probably under the same influence of differential growth. However, there is a much greater chance of error in measuring lipid weight or oxygen consumption, than there is in measuring total weight or carapace length. Therefore, the standard regression calculation has been made with the more erratic variable being the dependent one. This method has been used for morphological allometry as well, but here the very high correlation coefficients make it unlikely that any serious error is introduced by not using standard allometric methods (for review see Kidwell and Chase, 1967).

In the case of morphological allometry, both a and b are useful in describing growth stages, and both have been reported for many Maiid crabs (*e.g.,* Hartnoll, 1963). In the case of physiological allometry, the comparisons between variables are made on the basis of the slopes (a); testing the similarity of differential growth. The value of b has no meaning when compared here between different variables since it is based on different units and origins. But, when a single variable is compared throughout different growth stages, the value of b represents relative levels of usage in each stage. (Conversely, in this case a has little meaning.)

Morphological. Three identifiable growth stages exist in Maiid crabs; immature, prepubescent, and mature (Hartnoll, 1963). These stages are identified by two important points during the growth of the animal (Teissier, 1935): (1) the molt of prepuberty, where the immature proportions of the crab begin their transformation into those of the adult. This point is marked by an inflection in the allometric line, and is coincident with the first appearance of gonads. Vernet-Cornubert (1958), working with *Pisa tetraodon*, showed that this inflection appears at varying individual sizes. (2) The molt of puberty, or in Maiid crabs, the terminal molt (Carlisle, 1957); at this point the crab is fully mature and the plot of allometric lines exhibits a discontinuity representing the terminal changes in proportions.

The most striking morphological allometries in crabs are those between the length of the male chelipeds (or propodus thereof) and the length of the carapace; and the width of the female abdomen, and the width of the carapace. These measurements were used after the fashion of Teissier (1960) and Hartnoll (1963) to establish the three stages in this crab. Size measurements were made to the nearest 0.5 mm with a caliper.
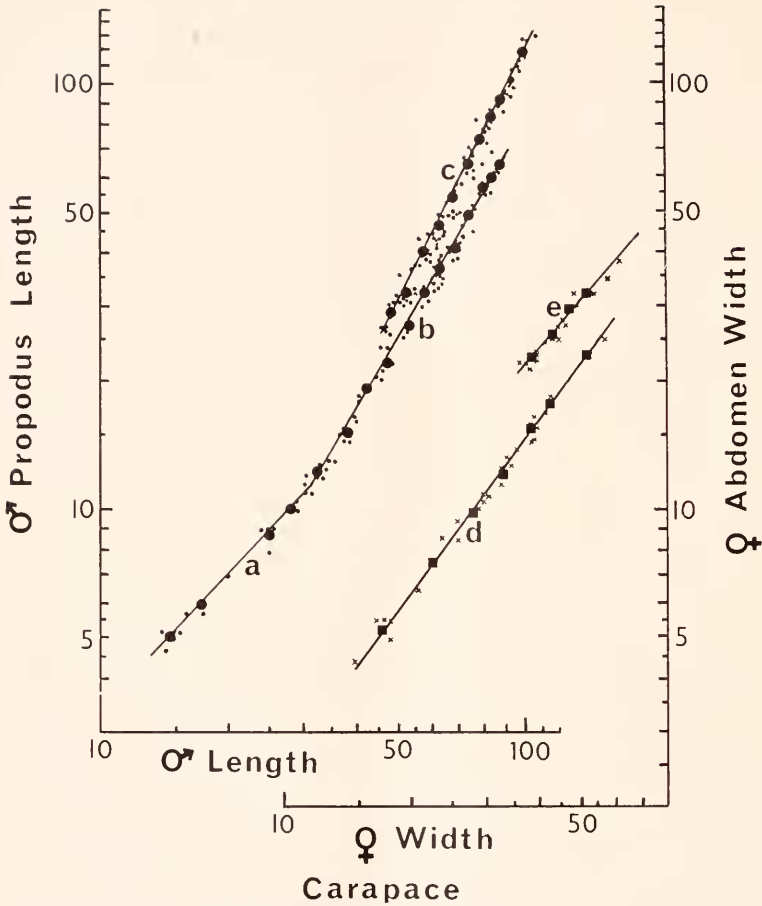
FIGURE 1. Morphological allometry, male propodus/carapace length and female abdomen/carapace widths. Lines are: males, "a" immature, "b" prepubescent, "c" mature; females, "d" immature-prepubescent, "e" mature. Small dots are individual values; large dots are size class averages.

In the case of the female abdomen/carapace allometry, the difference between molting and non-molting stages was apparent upon constructing a scattergram (Figure 1) and they could be collected into immature-prepubescent and mature stages for the computation of allometric constants. A preliminary computation based on size classes (shown in the figure) gave some hint of the prepubescent stage, but this was neither distinguishable in individual crabs nor statistically valid for the purposes of computing constants. The males presented a more difficult case, although the immature and prepubescent sizes were rapidly distinguishable in the scattergram, much of their size ranges intergraded imperceptibly. However, the smallest prepubescent and the largest mature sizes were evident beyond the intergrading region, and the very smallest mature sizes were identified by their mature gonads and also by their having three layers of barnacles, an indica-

tion that they had not molted for several years (Hartnoll, 1963). (The subtidal barnacle found on these crabs, *Balanus amphitrite niveus*, sets only once each year according to Ray, 1959). These smallest and largest sizes were used as guides in drawing lines through the uncertain region, separating individual points into prepubescent and mature stages, with ambiguous points arbitrarily divided between the two lines. When all of the points had been assigned to their respective stages, final allometric constants were computed.

Stomach capacity. The maximum stomach capacity was estimated by plotting whole stomach weights (cardiac and pyloric regions together) both as found in newly-collected specimens and in some fed to satiety. Feeding was necessary in large crabs because they were never collected with full stomachs. After weighing whole, the stomachs were flushed and blotted and the empty weight recorded. Separate regression lines were computed for the maxium points, and for the empty points, the difference between these lines at a given size being taken as the maximum capacity. For purposes of computation, the specific gravity of stomach contents was considered to be unity so that one gram was equivalent to one cc of contained food.

Oxygen consumption. This was measured in closed containers, the dissolved oxygen not being allowed to decrease to less than $\frac{3}{4}$ of the ambient level (Stroganov, 1964). Measurements were obtained for the entire size range of *Libinia*, from newly-released zoeae, to the largest (450 g) mature males (Rathbun, 1925). Such a millionfold span of weight decreases the erratic value for a that can be found when using small ranges of weight (Hemmingsen, 1960). Large crabs were measured singly, crabs less than 5 g were measured in groups, and about a thousand zoeae were measured simultaneously. The length of the experiments varied from half an hour in the largest crabs (measured in a submerged wash basin with a plexiglas lid), to several hours in the smallest crabs (measured in submerged plexiglas boxes). These measurements were made only upon freshly-collected, non-molting specimens (23), and were considered to represent the routine rate (Bayne, 1973).

Hepatopancreas. This was weighed wet without draining, and portions of tissue frozen for later lipid analysis by the chloroform-methanol method of Folch, Lees and Sloane-Stanley (1957). Subsequent calculations were based on wet weight.

Stomach contents. The contents removed in the stomach capacity measurements were recorded as rough percentages in four categories: (1) Detritus, the flocculent upper 2–3 cm layer of muddy bottoms (Sanders, 1960). Because of the variability in published values for the organic content of this material, two samples were ashed giving an average organic (burnable) content of 1.83%. Figuring 4,000 cal/g (carbohydrate) this amounts to 73 cal/cc. (2) Algae, mostly fine filamentous rhodophyta and cholorophyta; as determined by ashing, their organic content averaged 7.5% of the wet weight. At 4,000 cal/g (Odum, 1963) this is an average of 300 cal/cc. (3) Invertebrates, primarily pelecypods and marine worms, indicated by valves and setae. An average dry weight of 20% was assumed, and multiplied by 5,700 cal/g (Brody, 1945) as protein, gives 1,140 cal/cc. (4) Flesh, this last general type consisted of small squid and fish and was figured at the same caloric value as (3). These percentages, multiplied by the weight of the contents gave the caloric value for each stomach examined.

The total weight of the contents was compared to the maximum capacity of the stomach, indicating the percentage of capacity used.

Feeding experiments. Four sets of feeding experiments were made having durations of 9–13 days. Crabs previously starved for up to two weeks were fed each day, uneaten food from the previous day being removed and weighed. The maximum rates of consumption were usually realized during the first day of the test, consumption declining rather steadily during succeeding days. Because they occur in groups under natural conditions, the crabs were fed in groups and the rates obtained are averages. These averages are expressed as multiples of the maximum stomach capacity (stomachsfull) eaten per day.

Assimilation efficiency. This was measured during the four sets of feeding experiments. Faeces were collected several times each day to prevent their possible consumption by the crabs (never observed). The crabs defecated immediately upon their first feeding, therefore the faeces produced on a given day might be the result of an earlier feeding. Faeces output, like food consumption, declined from a maximum during the first days, and the two rates were in proportion, but with the faeces output lagging behind food consumption by 2–3 days. Because of this lag, overall assimilation efficiencies were computed for each experiment on the basis of the total dry weights of food consumed and faeces produced.

TABLE 1

Allometric constants for the equation: log Y = $a$log X + log b; and a = the slope of the line, b is the intercept when X = 1; R = correlation coefficient

Stage	a	b	R
(a) Morphological allometry			
Males: Carapace/propodus lengths			
Immature	1.08	−0.56	0.9934
Known prepubescent	1.61	−1.36	0.9660
All prepubescent	1.72	−1.53	0.9915
Known mature	1.98	−1.89	0.9956
All mature	1.95	−1.85	0.9830
Females: Carapace/abdomen widths			
Immature	1.28	−0.86	0.9898
Prepubescent	1.35	−0.95	0.9854
Mature	1.12	−0.42	0.9791
(b) Physiological allometry			
Stomach fullness/live weight			
All immature full	0.80	−1.37	0.7901
All immature empty	0.97	−2.00	0.9058
Mature female full	1.01	−1.71	0.8190
Mature female empty	1.31	−2.77	0.9234
Mature male full	0.51	−0.94	0.8108
Mature male empty	0.78	−1.87	0.9096

TABLE II

F tests of regression lines showing; f values for a and b (slope and level), degrees of freedom, and level of significance (1%, 5%, X = not significant)

Pair of lines tested	a (slope)			b (level)		
	f	d.f.	Sig	f	d.f.	Sig
(Male propodus)						
Immature/known prepubescent	25.4	1/35	1	8.77	1/36	1
Known prepubescent/known mature	8.79	1/51	1	33.4	1/52	1
All prepubescent/all mature	24.5	1/183	1	237	1/184	1
(Female abdomen)						
Immature/prepubescent	0.646	1/24	X	0.891	1/25	X
Prepubescent/mature	7.48	1/31	5	539	1/32	1
Immature-prepubescent/mature	3.47	2/42	5	274	2/44	5
(Stomach weights)						
All maximum/all empty	0.491	1/11	X	2376	1/12	5
Immature as found/immature empty	0.543	1/22	X	6.00	1/23	5
Mature female as found/m.f. empty	5.03	1/36	5	72.9	1/37	5
Mature male as found/m.m. empty	1.00	1/18	X	84.3	1/19	5
(Hepatopancreas)						
Immature wet wt/all mature wet wt	0.039	1/56	X	12.7	1/57	5
Imm. lipid wt/all mature lipid wt	0.162	1/56	X	9.89	1/57	5
Routine O$_2$/imm. hepato. wet wt	1.06	1/44	X	153	1/45	7
Routine O$_2$/imm. lipid wt	0.267	1/47	X	—	—	—
Routine O$_2$/all stomach empty wt	0.083	1/63	X	—	—	—

RESULTS

Morphological allometry

The plots of male propodus/carapace lengths, and female abdomen/carapace widths are given in Figure 1, where both individual points (small dots) and size class averages (large dots) are shown. For purposes of computation the males were divided into five categories: (1) immature; (2) known prepubescent (this excluded large doubtful cases); (3) known mature (small barnacled sizes and large crabs with extreme propodus lengths); (4) all possible prepubescent; (5) all possible mature. The allometric constants (Table Ia) were compared by F tests (Table II). The lines including the doubtful points were indistinguishable from those formed only by known points, therefore these all inclusive lines were used. Male immature, prepubescent, and mature stages were all significantly different in slope and level. The inflection at the molt of prepuberty occurs at the average carapace length of 31.5 mm, and is evident in the figure from the difference in slope between lines "a" (immature) and "b" (prepubescent). The mature crabs (line "c") range in length from 47.0 to 106.0 mm, their individual points making a line distinct from that of the prepubescent crabs, which are found up to 87.0 mm long.

Female crabs were divided into three categories for computation: (1) immature; (2) prepubescent; (3) mature. The molt of prepuberty was not significant (Table II), and immature and prepubescent females were treated together. This combined stage (line "d") was found up to the carapace width of 43.0 mm. Mature females were found over the width range of 37.0 to 62.0 mm (line "e"), and

were significantly different from the immature line. Expressed as carapace lengths for comparison to the males, these figures are 52.5 mm for line "d," and 42.0 to 77.5 mm for line "e."

The most distinct differences in the physiological constants were subsequently found between the molting (immature and prepubescent) and non-molting (mature) crabs, therefore immature and prepubescent crabs of both sexes are treated together in the following comparisons, with mature females and mature males treated separately for a total of three stages, equivalent to two major growth stanzas within each sex. The first stanza is immature, actively growing and found in an abundance of algal food. The second is mature, reproducing, non-growing, and found on relatively barren mud bottoms. (This second stanza might be termed a "life" stanza because there is no growth.) The planktonic larvae of a crab would form a third major growth stanza.

Physiological allometry

Oxygen consumption measurements gave an average routine rate of 4.7 ml O_2/hr for a crab of 123 g fresh weight, similar to other published values. Vernberg (1956) gives 3.2 ml O_2/hr for this weight of *L. emarginata,* and Zeuthen (1953) gives a general value for crustacea equivalent to 3.7 ml O_2/hr at this weight. The values found in the present study may be termed a lower range of the excited rate due to measuring after handling (Aldrich, 1974a). Odd, high values, probably representing elevated rates due to biological rhythms (Ansell, 1973; Aldrich, 1974b) were excluded from the calculation. The allometric constants for ml O_2/g/hr were: $a = 0.81$, $b = 0.89$, $R = 0.9950$. The slope (a) is in virtual agreement with the a of 0.80 found by Zeuthen (1953). The average daily caloric cost of maintenance was computed at 4.83 cal/ml O_2 (Brody, 1945) for a basal rate (the very lowest range of points in the overall regression) 80% of the routine rate.

Stomach weights are given for individual crabs in Figure 2. The regression of maximum full weights has the constants: $a = 0.80$, $b = -1.15$, $R = 0.9950$; and the regression of all empty stomachs has the constants: $a = 0.80$, $b = -1.89$, $R = 0.9566$. Thus the full and empty stomach weights bear a constant relationship to one another over a hundredfold range of body weight. Therefore the capacity of the stomach has a constant allometric relationship to the weight of the crab. The slope of this capacity regression is virtually the same as that of the routine metabolism (an F test showed no significant difference). Although this does not prove that metabolic rate is dependent upon the capacity of the stomach, it does indicate that these relationships are similarly constant with increasing weight, suggesting a functional correlation.

The percentage of the maximum stomach capacity used is not the same in the three stages (Figure 2). Within each stage there is a significant difference between the levels of "as found" and empty stomach weights (Table II, b values). Immature-prepubescent, and mature females appear to use almost the maximum capacity, but large mature males seem to use a decreasing proportion as they increase in size. This is reflected in the significantly different slopes of the male "as found" and empty regressions (Table II), a difference not found in other stages and implying the constancy of empty weights, but the relative decrease of
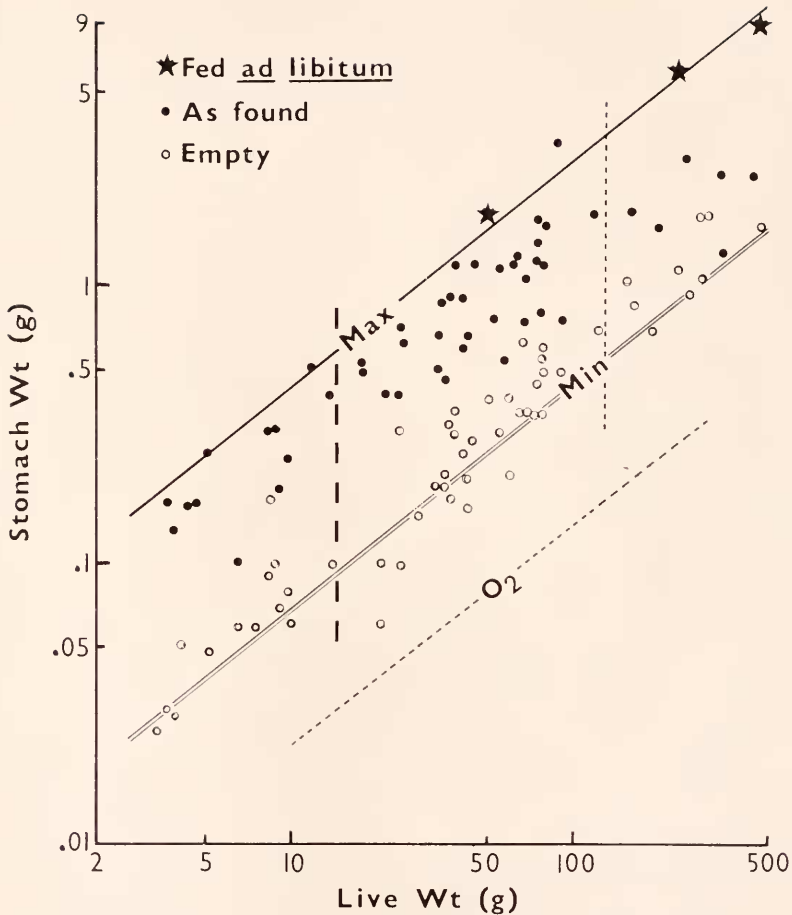
FIGURE 2. Stomach capacity and weight of contents found in collected crabs with maximum capacity = Max. line − Min. line at any given crab weight. Size ranges are: immature crabs to the left of the heavy dashed line; largest mature males to the right of the light dashed line; mature females and small mature males between the two dashed lines. Individual values both as found and when emptied are given. The regression of oxygen consumption is shown for comparison of slope, and is parallel to the regression of stomach capacity.

fullness with increasing size. Note the different empty stomach slopes (a in Table Ib) for the three stages and how their overall combination makes a "regular" allometric line parallel to that of the routine oxygen consumption.

The relationships of hepatopancreas total and lipid weights to total live weight are shown in Figure 3. Here immature-prepubescent crabs, as well as very large male crabs that have recently molted to maturity (Points "N") fall on the same regression line of hepatopancreas wet weight. The constants of this line are: $a = 0.82$, $b = -0.84$, $R = 0.9280$; therefore it is parallel to the regression of routine metabolism (an F test showed no significant difference in slopes, see Table II). The combined regression of mature male and female

hepatopancreas wet weight has the constants: $a = 0.86$, $b = -1.16$, $R = 0.8150$ and is not significantly different in slope from the previous regression, but is different in level. Thus the weight of the hepatopancreas follows the same allometric formula (slope of maximum weight) as the stomach capacity and routine metabolism, and again larger (mature) crabs have lower levels (b) of utilization of a physiological capacity. (That this drop in proportion is not due simply to the larger sizes of mature crabs is shown by the points "N" for very large newly-molted crabs.)

The total weight of lipid contained in the hepatopancreas follows an analogous pattern. Here the constants are: Immature-prepubescent, $a = 0.98$, $b = -2.08$, $R = 0.644$; all mature, $a = 1.16$, $b = 2.98$, $R = 0.5758$. F tests showed that these two lines are insignificantly different in slope, but again significantly different in level (Table II). Due to the great variability in individual values, an F test showed no difference between the immature-prepubescent slope and that of the routine metabolism.

The lower level of utilization of physiological capacity in mature crabs is again suggested by the caloric value of stomach contents (Figure 4). Here the caloric value decreases relative to the cost of maintenance as the size the crab increases,
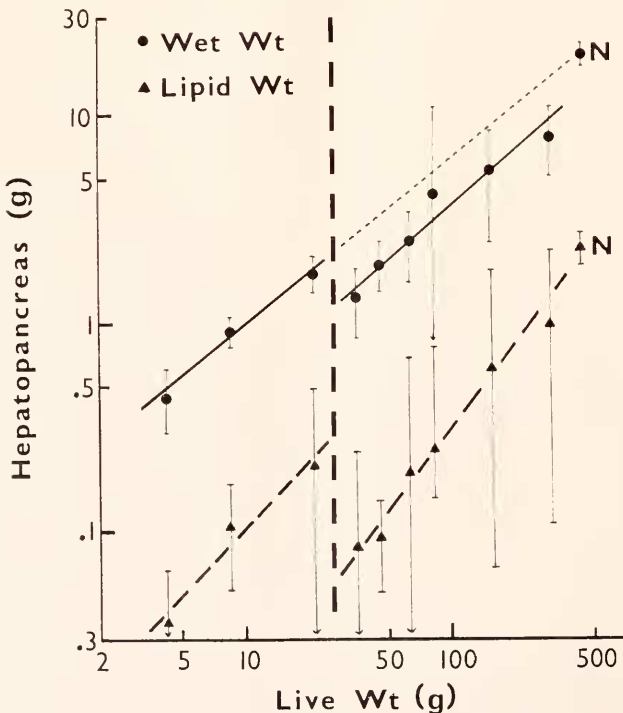

FIGURE 3. Hepatopancreas wet (total) weight (upper solid lines), and lipid weight (lower dashed lines). Data presented as size classes with standard deviations shown by the vertical bars. Crabs to the left of the vertical dashed line are immature-prepubescent, those to the right are mature (both males and females), the points "N" are recently molted males.
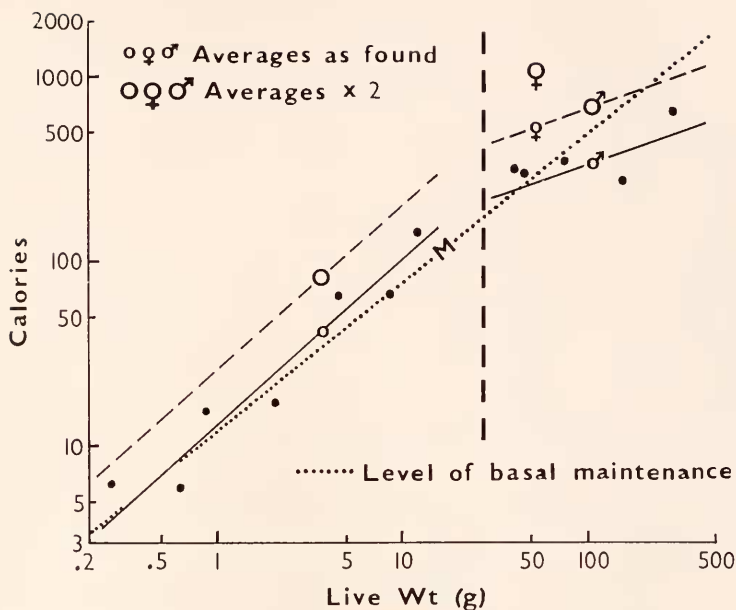
FIGURE 4. Caloric value of stomach contents found in collected crabs, contrasted with the caloric cost of basal maintenance. Crabs to the left of the vertical dashed line are immature-prepubescent, those to the right are mature. Data presented as size class averages (dots) and means (small symbols) for immature-prepubescent, mature females (mean only), and mature males. The effect of the cycling rate is shown by doubling the caloric values (large symbols and dashed regression lines).

especially in mature males. Again, immature crabs maintain a balance close to the maintenance cost, the regression of caloric values following the same slope as metabolism. Mature females also have a balance close to the maintenance cost. (The cost of monthly reproduction is less than that of rapid immature growth, Aldrich, 1972.) These trends suggested by the stomach contents are not as clear as the preceding ones due to the extreme variability in both the amount and caloric value of the contents (Table III), and the presentation is made without statistical significance (according to correlation coefficients). However, the trends agree with those previously found, the low caloric values for the mature males are especially marked, suggesting a real underutilization of stomach capacity.

The stomach content findings are complicated by the cycling rate, or multiples of stomach capacity (stomachsfull) that can be processed in a 24 hour period. In four sets of feeding experiments the maximum consumption in 24 hours averaged 1.95 stomachsfull (Table, IV). This means that the estimated maximum stomach capacity could be processed twice a day, or the cycling rate is such that any given contents could be digested within 12 hours. These figures were obtained with cleaned fish, mussels, and algae, all readily digestible. An earlier experiment (No. 5 in Table IV) where the crabs fed on starfish gave much the same result with this relatively undigestible food.

TABLE III

Percentage fullness (% of max. capacity) and stomach contents of crabs examined within 2 hours of collection

Size class (grams)	No.	Ave. % fullness	% Fullness acc. to food types			
			Detritus	Alga	Inverts.	Flesh
Immature males and females						
0.00–0.33	3	100		100		
0.34–0.67	2	50		50		
0.68–1.00	2	100		100		
1.1–3.3	8	56		50		6
3.4–6.7	8	75		65	10	
6.8–10	4	70		70		
11–33	1	100		100		
Mature females						
34–122	22	38	9	9	11	9
Prepubescent males						
14–74	5	46	4	23	19	
Mature males						
33–67	7	44	15	12	7	10
68–100	7	51	20	23		8
101–200	7	19	7	7	5	
201–500	5	14	4	10		

The assimilation efficiency averaged 96% (Table IV), so high that it was considered unity for purposes of calculations. There was no real difference in efficiencies whether the crabs were digesting animal or vegetable food. Such

TABLE IV

Feeding experiments showing average weight and number of crabs, food given (cleaned fish, mussel flesh, algae, and whole starfish), multiples of stomach capacity (stomachsfull) processed within 24 hours, and overall assimilation efficiencies

Exp. No.	Ave. Wt. ± S.D.	No. Crabs	Food	Multiple	Assim. Efficiency
1	5.8 ± 3.41	5	Fish, *Stenotomus*	1.53	96.5%
2	37.2 ± 6.59	10	Mussel, *Mytilus*	1.90	96.7%
3	45.0 ± 13.5	25	Fish, *Stenotomus*	2.05	99.3%
4	58.7 ± 10.1	8	Alga, *Codium*	2.31	95.0%
(5)	144 ± 169	16	Starfish, *Asterias*	(1.65)	—

high efficiencies are not uncommon in arthropods consuming animal food (Lawton, 1970, 1971).

DISCUSSION

As indicated by the scattergram (Figure 1), there is a considerable range of mature sizes in both males and females. For males, this range requires three molts at an average increase factor of 1.26 (Dyar's Law; Teissier, 1960). Two of these molts are optional in the sense that some prepubescent crabs exist in ever increasing sizes but still have not reached maturity as defined by the inability to undergo further molts. Because some of these larger prepubescent crabs appear to have mature gonads, "prepuberty" for them may include animals sexually mature before reaching their terminal anecdysis (Hartnoll, 1963). Some very large prepubescent males were kept in the laboratory tanks and they all molted in the autumn, whereas no mature crabs of any size ever molted. The consequence of the optical molts is a 16-fold weight range for mature, non-molting male crabs. This weight range is similar to that found for many other Maiid crabs (Hartnoll, 1963; Vernet-Cornubert, 1958), but was not anticipated since it is "common knowledge" that only the largest males are the mature sizes. Some of the smallest mature males were kept together with mature females and they actively pursued and mated with them, giving a behavioral confirmation of the status suggested by their allometry.

The lesser range of female mature sizes requires two molts, of which one would be optional. Smaller mature females were often collected bearing eggs, as well as the commoner ovigerous middle range, but none of the very largest mature females were collected with eggs. The reproductive status of these largest females crabs is therefore unclear.

Thus the morphological allometry made possible the recognition of this great range of mature sizes, leading apparently to quite different energetic requirements within the mature stage. Small crabs appear to live for several years when mature, as evidenced by their several layers of barnacles. Such crabs were usually collected in rocky habitats where food may have been more abundant than on the mud flats where the largest mature crabs were found. Large crabs were never found with more than a few scattered barnacles, an indication that they may not have lived as long as the small males. Two reproductive strategies may be available to Maiid crabs then; small size (and small numbers of larvae in the case of females) coupled with several reproductive years, and large size coupled with a shorter reproductive period. Although females will accept the smaller males as mates, the larger males have a distinct competitive advantage, when kept together in tanks during these experiments, they merely picked up and cast aside their smaller rivals.

Three major points recur in the physiological variables. First, the maximum capacity of the stomach, the maximum hepatopancreas weight, and the metabolic rate all follow the same slope (a) thus exhibiting similar physiological relationships at the maximum values. Secondly, regularly molting crabs exhibit high proportional usage of digestive capacity and hepatopancreas storage capacity as shown by their relatively high values of b (level). Thirdly, the mature stages (non-molting) are functioning at less than the maximum physiological capacity

for these factors. The weight and lipid content of the hepatopancreas, as well as the portion of stomach capacity used are lower than in the molting stage. This lower level of usage is reflected in their b values.

The calculated daily levels of caloric intake based on stomach contents could be doubled by assuming that these levels were processed twice daily, and that there was no correction for undigested food. This is probably an overestimate for the larger crabs since there would be no advantage in consuming less than the maximum possible in the food-poor habitat of the muddy bottoms. In this case the stomach contents may represent the actual daily consumption. However, doubling the caloric value of the stomach contents may be a good estimate for the growing stage. The great rate of growth (up to monthly doubling in weight) may require as much food as they can process and their algal habitat would supply it without limit.

Whatever the rate of processing stomach contents may have to do with their average "as found" level, the mature males appear to use less of their capacity as their size increases. Even doubling the caloric level of the contents leaves the largest males with an intake less than the minimum required for basal metabolism, as is shown in Figure 4 by the dashed lines through the average caloric values X 2. Further, mature females found in the same habitat are relatively better fed than the mature males. In the summer, females must bear the cost of monthly reproduction (Hinsch, 1968, 1972) and require more food than males, yet some specimens had up to three layers of barnacles, apparently indicating several years in the mature stage.

Although mature females may be relatively better feeders than males, it could be that mature males do not have an "inclination" to eat at a sufficient rate for long survival. Perhaps such large crabs, those that have passed through the optional molts, represent a specialized reproductive stage like spawning male salmon that never feed. This idea is strengthened by the large crabs not being found with layers of barnacles, suggesting that they do not live long. There may be a general reduction in feeding levels in mature crabs, at least during certain stages of reproduction. Pearson (1908) mentions that berried *Cancer pagurus* "feed very little," and Carlisle (1957) described the "heaps" formed by molting and mating *Mya squinado*, one persisting for two months. Presumably the crabs did not feed while in this stationary heap. (In this context, the author remembers as a little boy finding a heap of *Libinia*, a discovery rapidly abandoned.) The very small non-molting mature sizes were not examined separately and it would be instructive to see if there is a marked drop in their b values corresponding to that found in large mature sizes. This would show if there is a size effect within the mature stage or whether b values simply drop with the cessation of growth.

In all, the differences in b values between immature-prepubescent crabs (the first growth stanza) and mature ones (the second stanza) are significant and consistent throughout the variables compared. Because Maiid crabs do not molt when mature, this stanza is quite distinct and the size of the hepatopancreas may be a better indicator of relative energy demand than in brachyrhynchous crabs where molting continues through most of the reproductive life. One such brachyrhynchous crab, *Carcinus maenas*, exhibits seasonal fluctuations in metabolites stored in the hepatopancreas, but has no obvious storage of material in prepara-

tion for ecdysis, there being a marked variation between individuals in the later molt stages (Heath and Barnes, 1970). Seasonal fluctuations were not measured in *Libinia* and their effects may be important, but the molting cycle will not complicate the interpretation as it would in another brachyrhynchous crab, *Cancer pagurus* (Renuad, 1949). Whether or not the hepatopancreas does indicate relative energy demands, the level of stomach contents must indicate the rate of energy intake and this level is also shown to decrease in mature *Libinia*. The habitats defining the immature-prepubescent, and mature growth stanzas are different, and the rate of energy supply in the habitat of the mature crabs must be quite limited. As the points "N" in Figure 4 imply, the condition of newly-molted but very large mature crabs appears to be similar to a normal immature growing crab. However, the reserves are not maintained during subsequent life in the mature stanza. The capacity of the crab as a system probably remains unaltered, as is suggested by the similar *a's* for maximum stomach capacity and hepatopancreas weight. Thus the mature stage of this crab appears to be an underutilized end point of a system designed for the growth of the immature stage.

Summary

1. Allometric plots were used to separate *Libinia emarginata* into three male growth stages; immature, prepubescent, and mature; and two female stages; immature-prepubescent, and mature.

2. The existence of two optional prepubescent molts in males allows a 2.75-fold variation in mature (non-molting) length; and one optional molt in females allows a 1.75-fold variation in mature length.

3. Because of the very great size range in mature crabs (especially males), there are apparently two reproductive strategies; small mature size and several reproductive years, and large size with one reproductive year.

4. The regression of routine oxygen consumption, measured over the entire size range of this crab, exhibits virtually the same slope (0.81) as found by Zeuthen (1953) for crustacea in general.

5. The maximum capacity of the stomach, and the maximum hepatopancreas wet weight follow the same allometric relation (slope or a) as the oxygen consumption, in agreement with the idea that metabolic rate is reflected in the size of the digestive apparatus (Hemmingsen, 1950).

6. The actual weight of stomach contents, and the wet and lipid weights of the hepatopancreas (level or b) are not fixed and reflect relative energetic demands or availability.

7. During the stages undergoing regular molts (immature and prepubescent) these variables exhibit high level implying the maximal use of physiological capacity.

8. At the stage of maturity, these levels decrease relative to the growing stages, implying the underutilization of this capacity.

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